

Introduction



Cite this article: French JC, Riris P, Fernández-López de Pablo J, Lozano S, Silva F. 2021 A manifesto for palaeodemography in the twenty-first century. *Phil. Trans. R. Soc. B* **376**: 20190707.
<http://dx.doi.org/10.1098/rstb.2019.0707>

Accepted: 7 October 2020

One contribution of 18 to a theme issue 'Cross-disciplinary approaches to prehistoric demography'.

Subject Areas:

behaviour, environmental science, evolution, genetics

Author for correspondence:

Jennifer C. French
e-mail: jennifer.french@liverpool.ac.uk

A manifesto for palaeodemography in the twenty-first century

Jennifer C. French¹, Philip Riris², Javier Fernández-López de Pablo³, Sergi Lozano⁴ and Fabio Silva²

¹Department of Archaeology, Classics and Egyptology, University of Liverpool, Liverpool, UK

²Institute for the Modelling of Socio-Environmental Transitions, Bournemouth University, Poole, UK

³I.U. de Investigación en Arqueología y Patrimonio Histórico, University of Alicante, Alicante, Spain

⁴University of Barcelona, Barcelona, Spain

id JCF, 0000-0001-5947-6669; PR, 0000-0003-4244-7495; JF-LdP, 0000-0002-6953-7004; SL, 0000-0003-1895-9327; FS, 0000-0003-1368-6331

1. Defining palaeodemography: aims and scope

Demography is the study of human populations and their structure, i.e. the composition of populations, and the subdivision of the metapopulation into smaller subunits. Palaeodemography refers to the study of the demography of ancient populations for which there are no written sources (broadly synonymous with 'prehistoric demography') [1]. Palaeodemography shares the core aims of its present-day counterpart, namely, to document and explain changes within, and variations between, the size and structure of human populations. However, by definition, no direct demographic data—equivalent to modern-day censuses or registration forms—exist for prehistoric populations. Instead, palaeodemographic information is derived from a wide range of proxies, which only indirectly inform on demographic processes and parameters.

Accordingly, at present, we consider palaeodemography to be less an independent field akin to demography proper, and more an interlinked set of cross-disciplinary interests sharing the common aims of reconstructing and analysing prehistoric population histories. Archaeology is presently driving this agenda as the primary discipline relevant to human prehistory. The archaeological record is the origin of most data gathered to explore prehistoric population change and to test competing hypotheses. Elsewhere, other established fields—most prominently genomics, (biological and evolutionary) anthropology and cultural evolution—exhibit a growing interest in palaeodemography. This is unsurprising: population size and structure, and the basic demographic parameters of mortality, fertility and migration that underlie them, deeply affect human societies in all times and places, and are therefore highly relevant to a wide array of research questions. Processes such as gene flow, social network scaling, cultural complexity, innovation and trait accumulation, environmental footprint and societal resilience both influence, and in turn are influenced by, population change across multiple parameters (e.g. [2–6]).

Researchers have long emphasized the benefits of a multi-proxy, cross-disciplinary approach to palaeodemography [7]. No single discipline or dataset can inform on all aspects of prehistoric demography nor at all spatial and temporal scales (table 1) and the shortcomings and limitations of individual palaeodemographic proxies are well documented, even if often overstated (e.g. [8–10]). Against the backdrop of the recent maturation of palaeodemographic method and theory, we take this opportunity to reflect on the state of the art, outline broader ambitions for palaeodemography, and identify concrete challenges for future research to address; our 'manifesto' for palaeodemography in the twenty-first century, the central premise of which is that the future of prehistoric demographic research lies in the *combination* of data sources, methods and theories engendered by palaeodemography. Synthetic approaches provide both a more encompassing picture of prehistoric demography and a means of cross-checking the validity of palaeodemographic reconstructions and interpretations. Here, we take this emphasis one step

Table 1. The three main disciplinary sources of palaeodemographic data and the demographic variables on which they can inform.

field	data sources	demographic variables	scale of analysis
archaeology	radiocarbon dates, settlement data (room counts, site numbers, settlement phasings), material culture	population size, density, distribution, growth	regions, continents, cultures, food production systems over multi-centennial timescales and above
genomics/genetics	modern and ancient DNA	population size, admixture, migrations	multi-scalar, depending on sampling strategy
biological anthropology (skeletal palaeodemography)	biological remains including dental and skeletal samples	age-at-death distributions, population structure (age–sex distribution), fertility, life-history variables, causes of death, morbidity	local (cemeteries) to continental/global (palaeodemes) intra- and inter-generational time

further. As exemplified by the papers assembled in this issue, we propose that palaeodemography is *necessarily* cross-disciplinary.

The papers collected in this special issue of *Philosophical Transactions of the Royal Society B* stem from a pair of international workshops hosted in Tarragona at the Institut Català de Paleoecologia Humana i Evolució Social (1–2 March 2018) and London at the UCL Institute of Archaeology (29–30 March 2019), after a conference session held during the 23rd European Association of Archaeologists meeting in Maastricht (31 August 2017). The three events shared the name *Cross-Disciplinary Approaches to Prehistoric Demography* (CROSSDEM), and now lend it to this issue. The workshops were sponsored, respectively, by the European Research Council and the Leverhulme Trust and the UCL Institute of Advanced Studies. At the time of writing, a third workshop is scheduled to take place in 2021 hosted by Aarhus University, in collaboration with the University of Cologne. Scholars at several other institutions have also expressed interest in hosting further CROSSDEM workshops. The popularity of the CROSSDEM endeavour reflects the wider growth in scholarly interest in the topic of prehistoric demography. It is this growth that motivated us to choose to write a manifesto for the future of palaeodemography to introduce this collection of papers.

2. State of the art in palaeodemography

To establish the background to our manifesto, here we summarize briefly the current state of the art in the main fields that contribute to palaeodemographic research. More thorough, general summaries of palaeodemography can be found in [1,11–16], including information on the historical development of approaches to the study of prehistoric demography.

(a) Archaeological proxies

Archaeological data are used primarily to reconstruct and analyse relative temporal and spatial trends in aggregate demographic measures (population density, size and distribution), ranging in scale from individual sites to continents. Archaeological approaches to palaeodemography fall into two broad groups: (i) those that assume a relationship between quantities of archaeological material and the intensity of past occupation/activity (a measure of population size and/or density), and

(ii) those that infer palaeodemographic trends from the cultural or environmental response to demographic change and/or that estimate demographic parameters from contemporary palaeoenvironmental and palaeogeographic reconstructions, usually in combination with demographic data from ethnographically documented subsistence-level societies. The first of these approaches currently dominates archaeological palaeodemographic research and is our focus here.

Georeferenced radiocarbon data, as a proxy for the relative change in activity over time, are presently the *de facto* first port of call for archaeologists conducting palaeodemographic research, as reflected in the contributions to this volume [17–21]. These works rely on summed probability distributions of calibrated radiocarbon dates (SPDs), although recently bootstrapped kernel density estimation has seen useful and increasing application [22,23] for analogous purposes: the aggregation of radiometric assemblages to reconstruct palaeodemography.

This trend, instigated by Berry [24] and more famously by Rick [25], is driven by the disciplinary ubiquity of radiocarbon dates and a growing literacy in computational methods, primarily the R statistical language [26], but also Python. That radiocarbon modelling dominates the archaeological discussion on demography appears to be a fair observation and should be acknowledged in the context of critiques levelled against the use of SPDs. Cautions against relying overly on radiocarbon to infer cultural processes are virtually as old as the method itself [27]. Current approaches are grounded in hypothesis testing and modelling uncertainty, and to suggest their use is inevitably problematic would be a disservice to the strides made and ongoing development of analytical frameworks [22,28–31]. Nonetheless, advances in methods that are on the horizon, which capitalize on Bayesian frameworks to overcome the intrinsic limitations of frequentist approaches, are highly promising for accurately resolving palaeodemographic parameters [32]. The recent publication of the IntCal20, SHCal20 and Marine20 curves will probably lead to further refinements, particularly in Pleistocene settings where dates are sparser [33].

Despite their ubiquity, the aggregate analyses of dates are not universally applicable as a robust palaeodemographic proxy. The half-life of ^{14}C precludes the use of radiocarbon dating beyond approximately 55 000 years ago. Human palaeodemographic studies before the second half of the

Late Pleistocene must seek alternative proxies, with an accompanying decrease in the temporal resolution available [34–36]. At the other end of the timescale, the preference for cross-referencing the archaeological record with numismatic data, high-quality seriations or written records in proto-historic (as well as historical) periods can also lead to the under-representation of radiocarbon dates, given their lower chronometric resolution. This form of investigation bias is known to produce artefacts in summary measures, for example, in the Roman period of Britain [37]. Nonetheless, aggregate analyses of ^{14}C dates are apparently sensitive to historical events of sufficient duration and intensity, some notable examples being the Black Death and First Nations oral accounts of ethnocide [23,38]. At present, equifinality of date assemblages and their possible (non-)response to such events must be evaluated on a case-by-case basis. There is, consequently, great potential in developing rigorous approaches that can distinguish the effects of systematic under sampling from a genuine dearth of archaeological deposits.

Archaeological alternatives to ^{14}C -based proxies include; settlement residency estimates—for example, numbers of assemblages, densities of archaeological material, size of sites and catchments areas—whose implementation varies considerably between mobile [35,39] and sedentary societies [40]; tree-ring dating ([41] this volume) and; historical documentation including death registers, population censuses and epigraphy [42,43]. Combining one or more of these diverse datasets with date assemblages provides useful controls on the limitations of radiocarbon summaries mentioned above [44]. In ancient urban contexts, modelling palaeodemographic parameters is rarely an end unto itself, usually forming an intermediate step for applications of theory that engages with the emergent socio-political properties of dense populations [18,45,46].

(b) Genomic proxies

Demographic history is one of the key variables influencing genetic variation. Inter and intra-population genetic variation and diversity are largely attributable to differences in ancestry and are driven by demographic processes. The spread and prevalence of genes are intrinsically related to patterns and rates of fertility and mortality (surviving into adulthood to be able to reproduce). Additional demographic variables affecting whom people have children with are also important (e.g. the rate of migration between populations).

Genetic variation and diversity tell us about three demographic variables and processes that are largely unferable from other palaeodemographic data sources: effective population size (N_e —an idealized measure equivalent to the number of reproducing individuals in a population), admixture and migration. There are two types of genetic data relevant for reconstructing prehistoric population histories: genetic data from living individuals/contemporary populations (modern DNA), and ancient DNA (aDNA) obtained directly from prehistoric fossil remains.

Genetics is the fastest growth area within palaeodemography. Much of this growth is attributable to the continued increase in data availability. Recent advances in sequencing and genotyping technologies (advances that have simultaneously lowered the costs of generating genetic data) have resulted in the creation of large, high-quality genomic

databases of present-day populations [47]. The development of next-generation sequencing (NGS) and high-throughput sequencing (HTS) methods have similarly increased the availability of ancient genetic data. In addition to reducing the costs of DNA retrieval, and the size of the archaeological/palaeontological sample required for extraction, these methods allow for the retrieval of whole-genome data [48,49]. In contrast to the earlier polymerase chain reaction method that could only reliably target the longest DNA sequences in ancient samples—usually restricted to multi-copy mitochondrial sequences [50]—NGS/HTS methods allow for the targeting of the shorter and more degraded autosomal DNA molecules, which are more representative of the whole genome, and provide a more complete record of genetic inheritance than uniparentally inherited loci (currently, the oldest autosomal hominin aDNA sequences retrieved come from the approximately 400 000-year-old pre-Neanderthal populations at Sima de los Huesos [51]). Concurrently, new protocols to both prevent and detect contamination of archaeological samples have also been developed, particularly those that detect contamination from modern human DNA [52,53]. The emerging field of palaeoproteomics (the study of ancient proteins) also provides insights into some variables relevant to demography—most notably phylogeny—with ancient proteins providing an alternative source of biomolecular data in contexts where ancient DNA has already degraded beyond retrievability [54].

The increase in high-quality genetic data does not in and of itself equate with a better understanding of prehistoric population histories. As with all sources of palaeodemographic data, genetic data only provide indirect information of past demographic patterns and processes, and issues of equifinality abound. Genetic variation is not just the result of past demographic histories—migrations, expansions and colonizations—but also of the mechanisms underlying genetic inheritance; random mutations, genetic drift and natural selection [55]. Several different population histories can be consistent with observed genetic diversity. Conversely, the same population history can give rise to different genetic patterns [56]. As reviewed by Loog in this volume [57], reconstructing past demography using genetic data (both ancient and modern) requires an inferential approach that compares patterns of genetic variation with model expectations from theoretical population genetics. These approaches divide into two broad categories: pattern-based, descriptive approaches, and explicit models. We refer the reader to Loog's paper for a thorough up-to-date summary of current approaches to demographic and palaeodemographic inference from genetic data.

(c) Osteological proxies (skeletal palaeodemography)

Skeletal data are the most direct form of palaeodemographic evidence, able to inform on demographic parameters at the level of the individual and on population dynamics at a comparatively higher level of spatial resolution. The two main measures of population composition, and the determining factors of most demographic behaviours, are age and biological sex: individual attributes that are ascertainable from human skeletons and from which demographic profiles and parameters of prehistoric populations can be generated. Skeletal palaeodemography is reliant on a principle of demographic uniformitarianism for both its theoretical and methodological

foundations—the assumption that both demographic processes and biological markers for inferring age and sex are universal across human populations and through time [58,59].

McFadden's contribution to this volume [60] summarizes succinctly both the history of skeletal analysis in palaeodemography and prevailing approaches, to which we refer the reader. In brief, her review of the state of the art of this subfield emphasizes recent methodological developments in two crucial areas: (i) the improvement of estimation methods and statistical procedures to calculate both individual age-at-death and the age-at-death distribution of skeletal assemblages (as laid out in [61]), and (ii) the development of new demographic proxy estimators. This latter development is particularly noteworthy. The use of proxy estimators reduces the influence of potentially inaccurate age estimates on the resultant demographic signature by minimizing the number of age categories and the corresponding number of points for potential error [62]. Furthermore, the skeletal data themselves provide the measured demographic rate, rather than life table data from hypothetical or historical populations; data that risk introducing inaccuracies owing to their in-built assumption of stationarity (defined as a population that is closed to migration, and with stable age-specific fertility and mortality rates resulting in 0% growth; conditions that very few real populations meet). Demographic proxy estimators therefore provide the most robust—if somewhat generalized—skeletally derived palaeodemographic measures. An improved estimator for fertility [63] as well as new estimators for population increase [64] and for maternal mortality [65] are important recent additions to the skeletal palaeodemography toolkit, although the long-recognized problem of the distorting influence of the under-representation of infants and the elderly in skeletal assemblages [66] on the resultant demographic signature persists [67].

Outside of this 'formal' skeletal palaeodemographic analysis, the human skeleton also provides data on other variables relevant to prehistoric demography, including (some) causes of mortality, morbidity and health (palaeopathology) and life-history-related variables. Of these life-history-related variables, the increased analysis of the age-at-weaning of prehistoric children (a proxy for the inter-birth interval and a key determinant of overall fertility in non-contracepting populations; [68]) through trace element distributions and isotopic values of teeth is a particularly notable contribution to our understanding of demographic parameters among prehistoric populations (e.g. [69–71]).

3. Looking forward: grand challenges for palaeodemography

As is typical of any growing multi-disciplinary research endeavour, each of the fields described above has its own challenges and priorities moving forward. We do not presume to speak for specialists within each of these fields and direct the reader to the relevant papers discussed above to learn more about the specific methodological and theoretical concerns of each of these approaches. Here, we highlight the 'grand challenges' facing palaeodemographic research: those that unite practitioners across multiple fields and that several papers in this special issue address.

(a) Generating absolute estimates for demographic parameters

Perhaps the most notable challenge—and one that is oft-remarked by those new to palaeodemography and its results—is generating absolute estimates for demographic parameters. Frustratingly, this challenge also applies to the aggregate demographic outcomes of these parameters (population size, density and growth rate) that are the main variables of interest in palaeodemographic research and are more readily inferred from the proxy records discussed above. Absolute estimates are not a prerequisite for the study of prehistoric demography. They do, however, offer multiple benefits over relative trends, including permitting the closer examination of the relationship(s) between population and other socio-cultural variables (including their analysis within cultural evolutionary frameworks—see below). Methods for generating absolute estimates of prehistoric population parameters vary, but typically combine direct data from one of the disciplines discussed above with quantitative demographic data from recent small-scale or subsistence-level societies (e.g. [72–74]). The 'Cologne Protocol', summarized by Schmidt *et al.* in this issue [35] is the most robust method for producing absolute demographic estimates from archaeological data, quantifying prehistoric population sizes and densities using a combination of geospatial analysis and demographic data from ethnographically documented foraging and/or farming groups. Originally developed for application to sedentary societies, the Cologne Protocol has subsequently been adapted for use on mobile populations and applied to multiple periods of European prehistory from the Upper Palaeolithic to the Iron Age (references in [35]) and modified to aid wider geographical applicability [39].

One of the advantages of the 'Cologne Protocol' is the scalability of its estimates from the regional to the supra-regional level; an important methodological advantage in a research area where the transfer of estimates of prehistoric population size and density across different spatial scales remains difficult [75]. More widely, integrating data that inform on prehistoric demography at disparate temporal and spatial scales (table 1), and combining these with models and data from present-day demography and ecology, is an ongoing challenge in the pursuit of an inherently multi-proxy cross-disciplinary palaeodemography. Failure to recognize these different scales can lead to misinterpretations of the data. A good case in point is the 'forager population paradox' [76]; the differences in population growth rate estimates between those recorded among recent hunter-gatherers and those estimated for prehistoric hunter-gatherers based on back-projections of known global population sizes. One possible solution to this paradox is that prehistoric and recent hunter-gatherers are demographically different (although as French & Chamberlain [59] show, this interpretation violates the principle of demographic uniformitarianism that underlies all palaeodemographic research). A more persuasive solution, as presented by Tallavaara & Jørgensen [42] in this volume, relates to the differences in temporal scale inherent in the data on population growth rate(s) of past and present hunter-gatherers. By comparing growth rate estimates derived from historical sources (Sámi tax records) with growth rates derived from simulated SPDs, reproducing the Belovsky's model of oscillating population dynamics [77] under different regimes of environmental productivity, Tallavaara and Jørgensen show that historical/ethnographic and

archaeological sources are actually measuring different parameters. While the former are recording actual changes in population size, archaeological data are not of sufficient resolution to detect comparable population dynamics and instead track long-term mean variance in population size controlled by environmental productivity.

(b) Definition and delimitation of ‘population’

In addition to differences in temporal and spatial scale, different disciplines and proxies vary in how they define and use ‘population’ as a unit of analysis, which must be taken into account when integrating data from multiple proxies. In archaeology, populations are defined as the people present within an area over a given period; the ‘census’ (N_c) or ‘on the ground’ population. By contrast, within genetics, populations are defined and measured via the relatedness and similarities between individuals (and by extension, the populations to which they belonged) and population size refers to effective population size (N_e). As such, estimates of past population size from genetic data on the one hand, and archaeological data on the other, are not directly comparable. Confusion over the difference between census and effective population size, and how the two measures relate to each other, may be partly responsible for the ambiguity and debate surrounding the empirical evidence of the relationship within cultural evolutionary frameworks between population size and cultural complexity—a topic reviewed expertly by Strassberg & Creanza in this volume [78].

At a more fundamental level, identifying or demarcating prehistoric ‘populations’ continues to challenge palaeodemographers. One archaeological means of recognizing a ‘population’—through material culture—embodies these challenges. The idea that material culture patterning corresponds to past populations is both long-standing and heavily debated with archaeology (e.g. [79]). This approach assumes (frequently more implicitly than explicitly) that spatial and temporal typological variation in material culture assemblages (stone tools/lithics, ceramics etc.) can demarcate and identify past populations. These variants are usually grouped into discrete ‘technocomplexes’: cultural taxonomic units with which populations (sometimes in the form of self-conscious ‘ethnic groups’) are frequently equated (i.e. people who manufactured stone tools attributed to the Aurignacian technocomplex become ‘the Aurignacians’). There are several problems with this approach, not least that many technocomplexes as ill-defined, historically contingent, and poor descriptors of spatial and temporal variability of assemblages [80,81]. As Bevan & Crema demonstrate in this issue [82], the temporal component of these technocomplexes—which often act as shorthands for periodizations—can furthermore distort any long-term reconstructions of population trends when they are used as the chronological framework.

The methodological limitations of these technocomplexes as ‘modifiable reporting units’ [82] in palaeodemography aside, if we assume that cultural traits are socially transmitted—that ‘ways of doing things’ are learnt by people from others in their society [83]—some association between specific attributes of material culture and specific populations should exist, although the nature and strength of this relationship is context-dependent. The development of methods to relate material culture variability to demography is a key priority for archaeological palaeodemography, particularly in earliest prehistory (Palaeolithic) where the archaeological record is more limited and consists primarily of lithics (stone tools). A growing

body of research drawing upon cultural evolutionary models uses temporal and spatial patterning in multiple lithic attributes to identify instances of migration and population interaction, and the structure of Palaeolithic populations (i.e. the way(s) in which the metapopulation was spatially segregated into sub-populations) (e.g. [84,85]). One key finding of these studies is that clusters (i.e. population groupings) often crosscut those based on traditional technocomplexes.

(c) Integration of non-demographic datasets

The challenges facing palaeodemography extend beyond the reconstruction of past population trends to analysing the consequences and drivers of prehistoric population change. In addition to the multi-proxy approach to generating palaeodemographic data, this analysis requires the development of methods to test and examine these data against non-demographic datasets. Setting trends in human demography against palaeoenvironmental and climatic records is a widespread practice (e.g. [37,86–89]), and comparisons between radiocarbon time series and independent environmentally or archaeologically derived proxies for human activity also offers interesting new directions [44,90–94]. Where sufficiently resolved data are available, correlations (or the lack thereof) between proxies may be explicitly tested for in a similar vein to established hypothesis-testing frameworks [95]. Consequently, we believe that radiocarbon-based methods will have an enduring place among palaeodemographic proxies. We also anticipate this role will be augmented, rather than diminished, by being cross-referenced with datasets and models generated by other approaches, in particular population and behavioural ecology.

Several papers presented here embody the potential different ways in which the dynamic relationship between population size and ecology were articulated in the past, specifically as regards environmental carrying capacity. McLaughlin *et al.* [19] analyse demographic changes during the Late Glacial and Early Holocene in Atlantic Iberia, an area dramatically impacted by postglacial eustatic changes and climatic-induced shifts in upwelling patterns. The adoption of a multi-proxy approach allowed for the study of long-term changes in population density against shifts in settlement organization and diet. The study clearly shows population growth during the Mesolithic favoured by an increase in environmental carrying capacity, especially in estuarine areas, prompting an increasing dependence on marine and estuarine food sources. Vander Linden & Silva [21] explore the relationship between population dynamics and farming dispersals. While the relationship between density-dependent population growth and human dispersals is a classic topic in population ecology, the originality of this contribution lies in the implementation of a new methodology to detect deviations from a model of density dependence in an archaeological context. The paper by Arroyo-Kalin & Riris [20] reconstructs prehistoric demography of the South American tropical lowlands during the Late Holocene (between 1050 BC and AD 1500). The examination of aggregate patterns derived from SPD time series against their geographical distribution suggests that Amazonian populations reached carrying capacity in the final millennia before European Conquest and describes a long-term regime of logistic growth under a diversified tropical subsistence base. The coincidence of palaeodemographic patterns alongside geographical expansions of indigenous Amazonian language families highlighted by these authors suggests that socio-cultural data (such as historical linguistics)

might provide another source of proxies with which to cross-reference ancient population data. Notably, the paper by Roscoe *et al.* [18] investigates the effects of population density on political centralization, and ultimately, its role as a driver of ancient state formation. They focus particularly on the precocious emergence of complex societies on the desert coast of Peru against the backdrop of the rise in integrative (ceremonial) and productive (irrigation) infrastructure. The effects of increased population density are clearly not limited to generating power differentials among formerly unranked groups or individuals, but may be expressed in a range of material evidence from rates of cultural transmission to the chances of a variety of types of social encounter taking place [96,97].

In general, however, few studies have examined the interplay between palaeodemography and other dimensions of human sociality, including but not limited to linguistics, social network structure, and political organization. The fine scale of prehistoric social dynamics and how they articulate with population history are rarely preserved in any detail. However, in rare cases where preservation, sampling interval and chronological resolution can all be taken advantage of with appropriate analytical techniques, profound insights into prehistoric demography can emerge. Recent examples include marriage patterns and possible institutionalized inequality in the central European Bronze Age [98] and the emergence of a dynastic elite in early Neolithic Ireland, with striking evidence of anomalous mating patterns potentially sanctioned through the extant power structure of the time [99]. Exceptional examples such as these will probably never be the norm in palaeodemographic research, which will continue to focus on the shifts of averages over a great span of years, but they are illustrative of the limits of what is possible with current methods.

4. A manifesto for palaeodemography in the twenty-first century

To conclude, we present here our manifesto for palaeodemography in the twenty-first century—our recommendations of best practice and collegial suggestions for priorities for future research in palaeodemography, building on the work presented in this special issue. While distinct, each element of this manifesto is united by our central premise: that the future of prehistoric demographic research lies in the *combination* of data sources, methods and theories engendered by palaeodemography.

1. *Adoption of multi-proxy approaches.* Palaeodemographic parameters can be inferred from various sources, including ethnographic, genomic, historic and archaeological. All these proxies differ in scale, scope and sampling resolution. Adopting approaches combining several of these proxies can compensate for limitations of individual proxies and provide richer and deeper views of demography-related processes from the deep past.
2. *Discussion of underlying assumptions and elaboration of palaeodemographic models.* The data-driven nature of palaeodemographic research means that interpretation of results usually occurs within the wider framework of the mathematical and/or computational models employed. Discussion of the underlying assumptions and limitations of these models is vital to the assessment of the results and their interpretation and a necessary step in the improvement or elaboration of

palaeodemographic methods and databases. In particular, applying experimental approaches to explore quantitative models from population ecology (and related fields) and further actualistic and experimental studies of the key assumptions of these models (including, for example, the analysis of taphonomic loss under different kind of sedimentary regimes or modelling the effects of different mobility regimes on the accumulation of anthropogenic carbon) merit a special place in the future of palaeodemographic research, allowing for the improved testing of competing hypotheses and refining theoretical frameworks (see below).

3. *Development of a theory of palaeodemography.* Palaeodemography is not just a methodological endeavour; several of the challenges mentioned above also need to be considered theoretically. Issues such as whether and how demography impacts the quantity and patterning of settlements and radiometric dates are not merely epistemological but also ontological challenges. An ideal starting point is increased engagement with existing demographic and taphonomic theory; developing a more robust ‘middle range theory’ of palaeodemography, focusing on the nature of the relationship(s) between demographic parameters and the data we employ to infer them.
4. *Fostering cross-disciplinary discussions and initiatives.* The challenge of future palaeodemographic research is targeting scientific audiences from very different disciplines (archaeology, human biology, ecology, genetics). As with any other cross-disciplinary effort, this challenge requires setting multi-disciplinary discussion spaces to share research goals, concepts and methodologies. This is the approach adopted by the CROSSDEM initiative and exemplified by Shennan & Sear’s contribution to this volume [100] that combines perspectives from leading practitioners of archaeological demography and evolutionary demography, respectively.
5. *Adhering to the Open Science basic principles.* Because most of the present and future palaeodemographic research relies on data-driven approaches, the adoption of an Open Science framework is compulsory. This entails the full publication of data, metadata and methods allowing assessment of data quality and supporting research reproducibility. In particular, as exemplified by different papers from this special issue, the adoption of open-source statistical packages (such as R), as well as common repositories for quantitative methods and datasets (GitHub) has become a common practice in radiocarbon palaeodemography. Future research on other classes of archaeological datasets must seek to follow the same principles. Generally speaking, the acquisition of datasets for palaeodemographic research and the production of high-quality metadata needs to be considered a priority in future research agendas, which needs to be recognized by funding agencies.

Palaeodemography is an emerging field of inquiry in which the drive to historicize past events is juxtaposed—and often in conflict—with the search for evolutionary dynamics and long-term trends. At present, questions are in abundance; definitive resolutions or concrete answers less so. We argue that this open playing field should be seen as an opportunity to overcome past shortcomings, as we find our species at a point in history when the limits of ecological resilience have never been of greater concern. Societal and demographic collapse continue to loom large in both popular [101] and scientific imaginaries [102,103]. Malthus casts long shadows, and one only needs to consider

the identification of prehistoric boom and bust cycles as an example [104]. We envision that palaeodemography may one day provide a uniquely long-term foil to the more immediate and contemporary concerns of demography, *sensu stricto*. Our attention is drawn to the parts of the world for which no written census or population records exist, and the entire span of our genus' history since its emergence in Africa. The very nature of the archaeological and palaeoanthropological record means that inference becomes increasingly constrained the closer in time one gets to the dawn of what may be termed a 'human population' to study. Matching the resolution and sampling quality of modern population studies (be they ethnographic, archival, Western, educated, industrialized, rich and democratic (WEIRD) or otherwise based on observational data) in, for example, *Homo naledi* is in all probability a non-starter. As demonstrated by this collection of papers, however, palaeodemographic researchers across the world have the reach and ability to address profound questions across timescales that dwarf most demographic studies. In other words, we propose that palaeodemographic research must be pragmatic and focused in scope to mature as a field of inquiry. Our manifesto

establishes the guidelines for achieving this goal, and we hope to see it realized in forthcoming work.

Data accessibility. This article has no additional data.

Authors' contributions. All authors contributed to the conceptualization, writing and editing of this article.

Competing interests. We declare we have no competing interests.

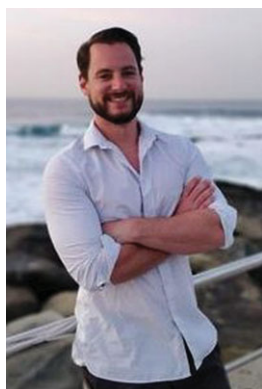
Funding. J.C.F.'s contribution was funded by a Leverhulme Trust Early Career Fellowship (grant number: ECF-2016-128), a Hunt Postdoctoral Fellowship from the Wenner-Gren Foundation (grant number: 9862) and the UCL Institute of Archaeology. P.R. was funded by a British Academy Postdoctoral Fellowship (PF2 \180065). J.F.-L.d.P. and S.L. have received funding from the European Research Council (ERC-CoG-2015) under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 683018). S.L. was also supported by the Research Group Economic History and Development (Industry, Business and Sustainability) (grant no. 2017 SGR 1466), and J.F.L.d.P. by the grant no. 2018/040 from the CIDEGENT programme of Generalitat Valenciana.

Acknowledgements. We thank all participants of the CROSSDEM workshops and other colleagues who have contributed to this special issue. Special thanks to the reviewers to whom all the contributed articles owe a great intellectual debt.

Editors' biographies



Jennifer C. French is a Lecturer in Palaeolithic Archaeology in the Department of Archaeology, Classics and Egyptology, at the University of Liverpool, UK. She received her PhD from the University of Cambridge in 2013. From 2012 to 2016, she was a Junior Research Fellow in Archaeology and Anthropology at Peterhouse, Cambridge, and in 2016 moved to University College London to take up a Leverhulme Trust Early Career Fellowship. Her research focuses on the reconstruction of demographic changes among the Palaeolithic hunter-gatherer populations of Europe and their interpretation within wider Pleistocene social and climatic contexts.



Philip Riris is a Lecturer in Archaeological and Palaeoenvironmental Modelling at the Institute for Modelling Socio-Environmental Transitions, Bournemouth University, UK. He earned his PhD from the University of Southampton in 2015. Between 2015 and 2019, he held postdoctoral positions at the Institute of Archaeology, University College London, latterly a British Academy Postdoctoral Fellowship, as well as a Visiting Fellowship at the Sainsburys Centre for Visual Arts, University of East Anglia. His research focuses on socio-environmental relationships in the ancient past, in particular population history, food production systems and landscape archaeology in tropical South America. He has also contributed towards rock art studies in the Amazonian and Orinocan lowlands.



Javier Fernández-López de Pablo is a Distinguished Researcher at the University of Alicante, Spain. He received his PhD at the University of Alicante in 2005, completed his postdoctoral training at the Department of Anthropology at the University of California Santa Barbara (2006–2009) and a Tenure Track 'Ramón y Cajal' position (2012–2016) at the Catalan Institute of Human Paleoecology and Social Evolution. His research focuses on the study of Late Pleistocene and Early Holocene socio-ecological dynamics, particularly testing demographically dependent models of cultural change in its ecological context.



Sergi Lozano is an Associate Professor at University of Barcelona, Spain. He received a PhD in ‘Sustainability, Technology and Humanism’ from the Polytechnic University of Catalonia (BarcelonaTech) in 2008. Between 2014 and 2018, he was a ‘Ramón y Cajal’ Research fellow at the Catalan Institute of Human Palaeoecology and Human Evolution (IPHES). His recent research efforts have focused on developing quantitative approaches to study long-term socio-economic and cultural phenomena, mainly based on historical and archaeological records.



Fabio Parracho Silva is a Lecturer in Archaeological Modelling at the Institute for Modelling Socio-Environmental Transitions, Bournemouth University, UK. He has held a PhD in Astrophysics since 2010. He is the co-founder and co-editor of the *Journal of Skyscape Archaeology* and Secretary of the European Society for Astronomy in Culture (SEAC). His research is split between archaeoastronomy, landscape archaeology and the modelling of dispersal dynamics at large spatio-temporal scales, including dispersals of crops and cultural traditions.

References

1. Bocquet-Appel J-P. 2008 *Recent advances in paleodemography: data, techniques, patterns*. Dordrecht, The Netherlands: Springer.
2. Anderies JM. 2006 Robustness, institutions, and large-scale change in social-ecological systems: the Hohokam of the Phoenix Basin. *J. Inst. Econ.* **2**, 133–155. (doi:10.1017/S1744137406000312)
3. Bromham L, Hua X, Fitzpatrick TG, Greenhill SJ. 2015 Rate of language evolution is affected by population size. *Proc. Natl Acad. Sci. USA* **112**, 2097–2102. (doi:10.1073/pnas.1419704112)
4. David-Barrett T. 2019 Network effects of demographic transition. *Sci. Rep.* **9**, 2361. (doi:10.1038/s41598-019-39025-4)
5. Metcalf CJE, Pavard S. 2006 Why evolutionary biologists should be demographers. *Trends Ecol. Evol.* **22**, 205–212. (doi:10.1016/j.tree.2006.12.001)
6. Migliano AB *et al.* 2017 Characterization of hunter-gatherer networks and implications for cumulative culture. *Nat. Hum. Behav.* **1**, 2. (doi:10.1038/s41562-016-0043)
7. Paine R. 1997 The need for a multidisciplinary approach to prehistoric demography. In *Integrating archaeological demography: multidisciplinary approaches to prehistoric population* (ed. RR Paine), pp. 1–18. Carbondale, IL: Centre for Archaeological Investigations, Southern Illinois University of Carbondale.
8. Contreras DA, Meadows J. 2014 Summed radiocarbon calibrations as a population proxy: a critical evaluation using a realistic simulation approach. *J. Arch. Sci.* **52**, 591–608. (doi:10.1016/j.jas.2014.05.030)
9. Attenbrow V, Hiscock P. 2015 Dates and demography: are radiometric dates a robust proxy for long-term prehistoric demographic change? *Archaeol. Oceania* **50**(Suppl.), 29–35. (doi:10.1002/arco.5052)
10. Petersen W. 1975 A demographer's view of prehistoric demography (and comments and replies). *Curr. Anthropol.* **16**, 227–245. (doi:10.11086/201542)
11. Bocquet-Appel J-P. 2008 *La Paléodémographie. 99, 99% de l'Histoire Démographique des Hommes ou la Démographie de la Préhistoire*. Paris, France: Éditions Errance.
12. Chamberlain A. 2006 *Demography in archaeology*. Cambridge, UK: Cambridge University Press.
13. Drennan RD, Berrey CA, Peterson CE. 2015 *Regional settlement demography in archaeology*. Clinton Corners, NY: Eliot Werner Publications Inc.
14. Hassan F. 1981 *Demographic archaeology*. New York, NY: Academic Press.
15. Porčić M. 2016 *Paleodemography: a critical review of theory, methods and research*. Belgrade, Serbia: Faculty of Philosophy, Laboratory for Bioarchaeology, University of Belgrade. (Written in Serbian.)
16. Séguy I, Buchet L. 2013 *Handbook of paleodemography*. Dordrecht, The Netherlands: Springer.
17. Porčić M, Blagojević T, Pendić J, Stefanović S. 2021 The Neolithic Demographic Transition in the Central Balkans: population dynamics reconstruction based on new radiocarbon evidence. *Phil. Trans. R. Soc. B* **376**, 20190712. (doi:10.1098/rstb.2019.0712)
18. Roscoe P, Sandweiss DH, Robinson E. 2021 Population density and size facilitate interactive capacity and the rise of the state. *Phil. Trans. R. Soc. B* **376**, 20190725. (doi:10.1098/rstb.2019.0725)
19. McLaughlin TR, Gómez-Puche M, Cascalheira J, Bicho N, Fernández-López de Pablo J. 2021 Late Glacial and Early Holocene human demographic responses to climatic and environmental change in Atlantic Iberia. *Phil. Trans. R. Soc. B* **376**, 20190724. (doi:10.1098/rstb.2019.0724)
20. Arroyo-Kalin M, Riris P. 2021 Did pre-Columbian populations of the Amazonian biome reach carrying capacity during the Late Holocene? *Phil. Trans. R. Soc. B* **376**, 20190715. (doi:10.1098/rstb.2019.0715)
21. Linden MV, Silva F. 2021 Dispersals as demographic processes: testing and describing the spread of the Neolithic in the Balkans. *Phil. Trans. R. Soc. B* **376**, 20200231. (doi:10.1098/rstb.2020.0231)

22. Bronk Ramsey C. 2017 Methods for summarizing radiocarbon datasets. *Radiocarbon* **59**, 1809–1833. (doi:10.1017/RDC.2017.108)
23. McLaughlin TR. 2019 On applications of space–time modelling with open-source 14C age calibration. *J. Arch. Method Theory* **26**, 479–501. (doi:10.1007/s10816-018-9381-3)
24. Berry MS. 1982 *Time, space, and transition in Anasazi prehistory*. Salt Lake City, UT: University of Utah Press.
25. Rick JW. 1987 Dates as data: an examination of the Peruvian preceramic radiocarbon record. *Am. Antiq.* **52**, 55–73. (doi:10.2307/281060)
26. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
27. Willey GR. 1958 Estimated correlations and dating of South and Central American culture sequences. *Am. Antiq.* **23**, 353–378. (doi:10.2307/276486)
28. Timpson A, Colledge S, Crema E, Edinborough K, Kerig T, Manning K, Thomas MG, Shennan S. 2014 Reconstructing regional population fluctuations in the European Neolithic using radiocarbon dates: a new case-study using an improved method. *J. Arch. Sci.* **52**, 549–557. (doi:10.1016/j.jas.2014.08.011)
29. Crema ER, Habu J, Kobayashi K, Madella M. 2016 Summed probability distributions of 14C dates suggests regional divergences in the population dynamics of the Jomon period in eastern Japan. *PLoS ONE* **11**, 4. (doi:10.1371/journal.pone.0154809)
30. Brown WA. 2017 The past and future of growth rate estimation in demographic temporal frequency analysis: biodemographic interpretability and the ascendance of dynamic growth models. *J. Arch. Sci.* **80**, 96–108. (doi:10.1016/j.jas.2017.02.003)
31. Bevan A, Crema ER. 2020 rcarbon: methods for calibrating and analysing radiocarbon dates. 2020. See <https://github.com/ahb108/rcarbon>.
32. Price MH, Capriles JM, Hoggarth JA, Bocinsky K, Ebert CE, Jones JH. 2020 End-to-end Bayesian analysis of 14C dates reveals new insights into lowland Maya demography. *bioRxiv*, 185256. (doi:10.1101/2020.07.02.185256)
33. Reimer PJ. 2020 Composition and consequences of the IntCal20 radiocarbon calibration curve. *Quat. Res.* **96**, 22–27. (doi:10.1017/qua.2020.42)
34. Archer W. 2021 Carrying capacity, population density and the later Pleistocene expression of backed artefact manufacturing traditions in Africa. *Phil. Trans. R. Soc. B* **376**, 20190716. (doi:10.1098/rstb.2019.0716)
35. Schmidt I *et al.* 2021 Approaching prehistoric demography: proxies, scales and scope of the Cologne Protocol in European contexts. *Phil. Trans. R. Soc. B* **376**, 20190714. (doi:10.1098/rstb.2019.0714)
36. French JC. 2016 Demography and the Palaeolithic archaeological record. *J. Arch. Method Theory* **23**, 150–199. (doi:10.1007/s10816-014-9237-4)
37. Bevan A, Colledge S, Fuller D, Fyfe R, Shennan S, Stevens C. 2017 Holocene fluctuations in human population demonstrate repeated links to food production and climate. *Proc. Natl Acad. Sci. USA* **114**, E10524–E10531. (doi:10.1073/pnas.1709190114)
38. Edinborough K, Porčić M, Martindale A, Brown TJ, Supernant K, Ames KM. 2017 Radiocarbon test for demographic events in written and oral history. *Proc. Natl Acad. Sci. USA* **114**, 12 436–12 441. (doi:10.1073/pnas.1713012114)
39. Lundström V, Peters R, Riede F. 2021 Demographic estimate from the Palaeolithic–Mesolithic boundary in Scandinavia: comparative benchmarks and novel insights. *Phil. Trans. R. Soc. B* **376**, 20200037. (doi:10.1098/rstb.2020.0037)
40. Ortman SG. 2019 A new kind of relevance for archaeology. *Front. Digital Humanities* **6**, 16. (doi:10.3389/fdigh.2019.00016)
41. Robinson E, Bocinsky RK, Bird D, Freeman J, Kelly RL. 2021 Dendrochronological dates confirm a Late Prehistoric population decline in the American Southwest derived from radiocarbon dates. *Phil. Trans. R. Soc. B* **376**, 20190718. (doi:10.1098/rstb.2019.0718)
42. Tallavaara M, Jørgensen EK. 2021 Why are population growth rate estimates of past and present hunter–gatherers so different? *Phil. Trans. R. Soc. B* **376**, 20190708. (doi:10.1098/rstb.2019.0708)
43. Verhagen P, Joyce J, Groenhuijzen MR. 2019 *Finding the limits of the limes: modelling demography, economy and transport on the edge of the Roman Empire*. Dordrecht, The Netherlands: Springer Nature.
44. Palmisano A, Bevan A, Shennan S. 2017 Comparing archaeological proxies for long-term population patterns: an example from central Italy. *J. Arch. Sci.* **87**, 59–72. (doi:10.1016/j.jas.2017.10.001)
45. Hanson JW, Ortman SG. 2017 A systematic method for estimating the populations of Greek and Roman settlements. *J. Roman Archaeol.* **30**, 301–324. (doi:10.1017/S1047759400074134)
46. Ortman SG, Coffey GD. 2017 Settlement scaling in middle-range societies. *Am. Antiq.* **82**, 662–682. (doi:10.1017/aaq.2017.42)
47. Mallick S *et al.* 2016 The Simons genome diversity project: 300 genomes from 142 diverse populations. *Nature* **538**, 201–206. (doi:10.1038/nature18964)
48. Krause J, Pääbo S. 2016 Genetic time travel. *Genetics* **203**, 9–12. (doi:10.1534/genetics.116.187856)
49. Leonardi M *et al.* 2017 Evolutionary patterns and processes: lessons from ancient DNA. *Syst. Biol.* **66**, e1–e29. (doi:10.1093/sysbio/syw059)
50. Llamas B, Willerslev E, Orlando L. 2016 Human evolution: a tale from ancient genomes. *Phil. Trans. R. Soc. B* **372**, 20150484. (doi:10.1098/rstb.2015.0484)
51. Meyer M *et al.* 2016 Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. *Nature* **531**, 504–507. (doi:10.1038/nature17405)
52. Key FM, Posth C, Krause J, Herbig A, Bos KI. 2017 Mining metagenomics data sets for ancient DNA: recommended protocols for authentication. *Trends Genet.* **33**, 508–520. (doi:10.1016/j.tig.2017.05.005)
53. Llamas B, Valverde G, Fehren-Schmitz L, Weyrich LS, Cooper A, Haak W. 2017 From the field to the laboratory: controlling DNA contamination in human ancient DNA research in the high-throughput sequencing era. *Sci. Technol. Archaeol. Res.* **3**, 1–14. (doi:10.1080/20548923.2016.1258824)
54. Welker F. 2018 Palaeoproteomics for human evolutionary studies. *Quat. Sci. Rev.* **190**, 137–147. (doi:10.1016/j.quascirev.2018.04.033)
55. Jobling MA. 2012 The impact of recent events on human genetic diversity. *Phil. Trans. R. Soc. B* **367**, 793–799. (doi:10.1098/rstb.2011.0297)
56. Orlando L, Cooper A. 2014 Using ancient DNA to understand evolutionary and ecological processes. *Annu. Rev. Ecol. Evol. Syst.* **45**, 573–598. (doi:10.1146/annurev-ecolsys-120213-091712)
57. Loog L. 2021 Something hidden but always there: the assumptions underlying genetic inference of demographic histories. *Phil. Trans. R. Soc. B* **376**, 20190719. (doi:10.1098/rstb.2019.0719)
58. Howell N. 1976 Toward a uniformitarian theory of human paleodemography. *J. Hum. Evol.* **5**, 25–40. (doi:10.1016/0047-2484(76)90097-X)
59. French JC, Chamberlain AT. 2021 Demographic uniformitarianism: the theoretical basis of prehistoric demographic research and its cross-disciplinary challenges. *Phil. Trans. R. Soc. B* **376**, 20190720. (doi:10.1098/rstb.2019.0720)
60. McFadden C. 2021 The past, present and future of skeletal analysis in palaeodemography. *Phil. Trans. R. Soc. B* **376**, 20190709. (doi:10.1098/rstb.2019.0709)
61. Hoppa RD, Vaupel JW. 2002 The Rostock Manifesto for paleodemography: the way from stage to age. In *Paleodemography: age distributions from skeletal samples* (eds RD Hoppa, JW Vaupel), pp. 1–8. Cambridge, UK: Cambridge University Press.
62. Bocquet-Appel J-P, Masset C. 1982 Farewell to paleodemography. *J. Hum. Evol.* **11**, 321–333. (doi:10.1016/S0047-2484(82)80023-7)
63. McFadden C, Oxenham MF. 2017 The D0–14/D ratio: a new paleodemographic index and equation for estimating total fertility rates. *Am. J. Phys. Anthropol.* **165**, 471–479. (doi:10.1002/ajpa.23365)
64. McFadden C, Oxenham MF. 2018 Rate of natural population increase as a paleodemographic measure of growth. *J. Arch. Sci. Rep.* **19**, 352–356. (doi:10.1016/j.jasrep.2018.03.012)
65. McFadden C, Oxenham MF. 2019 The paleodemographic measure of maternal mortality and a multi-faceted approach to maternal health. *Curr. Anthropol.* **60**, 141–146. (doi:10.1086/701476)
66. Bello SM, Thomann A, Signoli M, Dutoir O, Andrews P. 2006 Age and sex bias in the reconstruction of past population structures. *Am. J. Phys. Anthropol.* **129**, 24–38. (doi:10.1002/ajpa.20243)
67. McFadden C, Oxenham MF. 2019 The impacts of underenumeration and age estimation error on the D0–14/D ratio and palaeodemographic measures. *J. Arch. Sci. Rep.* **23**, 57–61. (doi:10.1016/j.jasrep.2018.10.033)

68. Campbell KL, Wood JL. 1988 Fertility in traditional societies. In *Natural human fertility* (eds P Diggory, M Potts, S Teper), pp. 39–69. London, UK: Palgrave MacMillan.
69. Austin C *et al.* 2013 Barium distributions in teeth reveal early-life dietary transitions in primates. *Nature* **498**, 216–220. (doi:10.1038/nature12169)
70. Smith TM *et al.* 2018 Wintertime stress, nursing, and lead exposure in Neanderthal children. *Sci. Adv.* **4**, eaau9483. (doi:10.1126/sciadv.aau9483)
71. Tsutaya T, Yoneda M. 2015 Reconstruction of breastfeeding and weaning practices using stable isotope and trace element analyses: a review. *Am. J. Phys. Anthropol.* **156**, 2–21. (doi:10.1002/ajpa.22657)
72. Birch-Chapman S, Jenkins E, Coward F, Maltby M. 2017 Estimating population size, density and dynamics of pre-pottery Neolithic villages in the central and southern Levant: an analysis of Beidha, southern Jordan. *Levant* **49**, 1–23. (doi:10.1080/00758914.2017.1287813)
73. Gautney JR, Holliday TW. 2015 New estimations of habitable land area and human population size at the Last Glacial Maximum. *J. Arch. Sci.* **58**, 103–112. (doi:10.1016/j.jas.2015.03.028)
74. Porčić M, Nikolić N. 2016 The Approximate Bayesian Computation approach to reconstructing population dynamics and size from settlement data: demography of the Mesolithic-Neolithic transition at Lepenski Vir. *Arch. Anthropol. Sci.* **8**, 169–186. (doi:10.1007/s12520-014-0223-2)
75. Müller J, Diachenko A. 2019 Tracing long-term demographic changes: the issue of spatial scales. *PLoS ONE* **14**, 1. (doi:10.1371/journal.pone.0208739)
76. Blurton Jones N. 2016 *Demography and evolutionary ecology of Hadza hunter-gatherers*. Cambridge, UK: Cambridge University Press.
77. Belovsky GE. 1988 An optimal foraging-based model of hunter-gatherer population dynamics. *J. Anth. Arch.* **7**, 329–372. (doi:10.1016/0278-4165(88)90002-5)
78. Strassberg SS, Creanza N. 2021 Cultural evolution and prehistoric demography. *Phil. Trans. R. Soc. B* **376**, 20190713. (doi:10.1098/rstb.2019.0713)
79. Roberts BW, Vander Linden M. 2011 *Investigating archaeological cultures: material culture, variability, and transmission*. New York, NY: Springer.
80. Reynolds N. 2020 Threading the weft, testing the warp: population concepts and the European Upper Palaeolithic chronocultural framework. In *Culture history and convergent evolution: can we detect populations in prehistory?* (ed. HS Groucutt), pp. 187–212. Cham, Switzerland: Springer.
81. Reynolds N, Riede F. 2019 House of cards: cultural taxonomy and the study of the European Upper Palaeolithic. *Antiquity* **93**, 1350–1358. (doi:10.15184/aqy.2019.49)
82. Bevan A, Crema ER. 2021 Modifiable reporting unit problems and time series of long-term human activity. *Phil. Trans. R. Soc. B* **376**, 20190726. (doi:10.1098/rstb.2019.0726)
83. Shennan S. 2002 *Genes, memes and human history. Darwinian archaeology and cultural evolution*. London, UK: Thames and Hudson.
84. Scerri EML, Groucutt HW, Jennings RP, Petraglia MD. 2014 Unexpected technological heterogeneity in northern Arabia indicates complex Late Pleistocene demography at the gateway to Asia. *J. Hum. Evol.* **75**, 125–142. (doi:10.1016/j.jhevol.2014.07.002)
85. Tostevin G. 2012 *Seeing lithics. A middle-range theory for testing for cultural transmission in the Pleistocene*. Oxford, UK: Oxbow.
86. Kelly RL, Surovell TA, Shuman BN, Smith GM. 2013 A continuous climatic impact on Holocene human population in the Rocky Mountains. *Proc. Natl Acad. Sci. USA* **110**, 443–447. (doi:10.1073/pnas.1201341110)
87. Santoro CM *et al.* 2017 Continuities and discontinuities in the socio-environmental systems of the Atacama Desert during the last 13,000 years. *J. Anth. Arch.* **46**, 28–39. (doi:10.1016/j.jaa.2016.08.006)
88. Fernández-López de Pablo J, Gutierrez-Roig M, Gomez-Puche M, McLaughlin R, Silva F, Lozano S. 2019 Palaeodemographic modelling supports a population bottleneck during the Pleistocene-Holocene transition in Iberia. *Nat. Commun.* **10**, 1–13. (doi:10.1038/s41467-019-09833-3)
89. Riris P, Arroyo-Kalin M. 2019 Widespread population decline in South America correlates with mid-Holocene climate change. *Sci. Rep.* **9**, 6850. (doi:10.1038/s41598-019-43086-w)
90. French JC, Collins C. 2015 Upper Palaeolithic population histories of Southwestern France: a comparison of the demographic signatures of 14C date distributions and archaeological site counts. *J. Arch. Sci.* **55**, 122–134. (doi:10.1016/j.jas.2015.01.001)
91. Tallavaara M, Pesonen P. 2018 Human ecodynamics in the north-west coast of Finland 10,000–2000 years ago. *Quat. Int.* **549**, 26–35. (doi:10.1016/j.quaint.2018.06.032)
92. Maezumi SY, Robinson M, de Souza J, Urrego DH, Schaan D, Alves D, Iriarte J. 2018 New insights from pre-Columbian land use and fire management in Amazonian dark earth forests. *Front. Ecol. Evol.* **6**, 00111. (doi:10.3389/fevo.2018.00111)
93. Feeser I, Dörfler W, Kneisel J, Hinz M, Dreibrodt S. 2019 Human impact and population dynamics in the Neolithic and Bronze Age: multi-proxy evidence from north-western Central Europe. *Holocene* **29**, 1596–1606. (doi:10.1177/0959683619857223)
94. Jørgensen EK, Pesonen P, Tallavaara M. In press. Climatic changes cause synchronous population dynamics and adaptive strategies among coastal hunter-gatherers in Holocene northern Europe. *Quat. Res.* (doi:10.1017/qua.2019.86)
95. Crema ER, Kobayashi K. 2020 A multi-proxy inference of Jomon population dynamics using Bayesian phase models, residential data, and summed probability distribution of 14C dates. *J. Arch. Sci.* **117**, 105136. (doi:10.1016/j.jas.2020.105136)
96. Smith ME. 2019 Energizing crowding and the generative role of settlement aggregation and urbanization. In *Coming together: comparative approaches to population aggregation and early urbanization* (ed. A Gyucha), pp. 37–58. Albany, NY: State University of New York Press.
97. Lozano S, Prignano L, Gómez-Puche M, Fernández-López de Pablo J. 2020 Early Holocene socio-ecological dynamics in the Iberian Peninsula: a network approach. In *Advances in social simulation* (eds H Verhagen, M Borit, G Bravo, N Wijermans), pp. 287–306. London, UK: Springer.
98. Mittnik A *et al.* 2019 Kinship-based social inequality in Bronze Age Europe. *Science* **366**, 731–734. (doi:10.1126/science.aax6219)
99. Cassidy LM *et al.* 2020 A dynastic elite in monumental Neolithic society. *Nature* **582**, 384–388. (doi:10.1038/s41586-020-2378-6)
100. Shennan S, Sear R. 2021 Archaeology, demography and life history theory together can help us explain past and present population patterns. *Phil. Trans. R. Soc. B* **376**, 20190711. (doi:10.1098/rstb.2019.0711)
101. Mann CC. 2018 *The wizard and the prophet*. New York, NY: Knopf Doubleday.
102. Rockström J *et al.* 2009 Planetary boundaries: exploring the safe operating space for humanity. *Ecol. Soc.* **14**, 32.
103. Nekola JC *et al.* 2013 The Malthusian–Darwinian dynamic and the trajectory of civilization. *Trends Ecol. Evol.* **28**, 127–130. (doi:10.1016/j.tree.2012.12.001)
104. Shennan S, Downey SS, Timpson A, Edinborough K, Colledge S, Kerig T, Manning K, Thomas MG. 2013 Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nat. Commun.* **4**, 1–8. (doi:10.1038/ncomms3486)